SELECTION OF VEGETATED HABITAT BY BROWN SHRIMP, *PENAEUS AZTECUS*, IN A GALVESTON BAY SALT MARSH

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ABSTRACT

Densities of the brown shrimp, *Penaeus aztecus*, in vegetated and nonvegetated habitats of a Galveston West Bay salt marsh were compared. Each of 81 sample pairs taken between 29 March and 23 July 1982 consisted of one sample from *Spartina alterniflora* habitat and another from nonvegetated habitat. Overall a mean density for shrimp of $11.7/m^2$ in vegetation was significantly greater than the mean density of $1.4/m^2$ in nonvegetated habitat ($P < 0.001$, t-test, 81 paired observations). In addition, shrimp densities varied according to a pattern of lower numbers and less apparent attraction to vegetation in the outer bayside part of the marsh to that of highest numbers and greatest attraction in the innermost marsh. Accordingly, respective means for the outer, middle, and inner marsh zones in vegetated/ nonvegetated sample pairs were 7.5/2.3, 11.0/1.0, and 16.6/0.6. Simple presence or absence of *S. alterniflora*, area covered by vegetation, and location within the marsh were the primary observed correlates to shrimp density patterns. Mean high water in vegetation was 22.1 cm compared with 41.8 cm for adjacent nonvegetated habitat, making vegetated habitat less accessible during periods of low water. Mechanisms that may have enhanced utilization of vegetated habitat for *P. aztecus* were reticulation in salt marsh macrostructure, relatively low tidal range, and seasonal periods of high water. The nursery function of the salt marsh was confirmed by dominance of small shrimp, with 95% of all individuals being smaller than 50 mm in rostrum through telson length. During April, the maximum mean density of postlarvae under 30 mm was $16.4/m^2$. Recruitment of postlarvae continued throughout the summer.

A $2.8m^2$ drop sampler, used to obtain the data, was found to be 2 to 5 times more effective for estimating densities of *P. aztecus* than trawls or seines. Consequently, our study improved the accuracy of estimates on estuarine shrimp densities, while also providing reliable evidence that *P. aztecus* may select for vegetated marsh habitat.

Estuaries have long been cited in their role as nurseries for penaeid shrimp (Anderson et al. 1949; Kutkuhn 1966; Thayer et al. 1978; Weinstein 1979). Growth and production of penaeids in estuaries have been associated with temperature (St. Amant et al. 1966; Zein-Eldin and Griffith 1966; Aldrich et al. 1968; Pullen and Trent 1969), salinity (Hildebrand and Gunter 1952; Gunter 1961; Barrett and Gillespie 1973; Browder and Moore 1981), and vegetation (Turner 1977; Faller 1979).

In salt marshes, vegetation may function variably to provide food, substrate, and protection for young penaeids. It is well known that *Spartina alterniflora* contributes to a detritus-based food web (Teal 1962; de la Cruz 1965) which at least potentially includes shrimp (Jones 1973). Microalgae and epibenthic biota associated with marshes may also serve in the food web (Haines 1977) and be used as food by foraging shrimp (Trent et al. 1969; Jones 1973). Since dense aquatic vegetation impedes certain predators (Vince et al. 1976; Nelson 1979; Coen et al. 1981; Heck and Thoman 1981), marsh grasses could also furnish protective cover for postlarval and juvenile penaeids. Unfortunately, our understanding of shrimp relationships to vegetation has been impaired by the inherent difficulty of sampling in marine vegetation.

Our aim was to overcome the sampling problem and to obtain accurate data on shrimp densities that could reliably depict differences between estuarine habitats. In the present study, *Penaeus aztecus* densities were compared between adjacent vegetated and nonvegetated habitats within a Galveston West Bay salt marsh. Since our experimental design incorporated paired sampling of habitats and samples with actual as opposed to relative numbers of shrimp, both the resolution

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and reliability of our analyses were improved over previous studies.

METHODS

Study Site

A salt marsh on the West Bay side of Galveston Island was selected as the study site (Fig. 1). The marsh extended into the island for about 2.5 km, allowing tidal circulation throughout numerous coves and bayous. The intertidal marsh was dominated by vegetation, *S. alterniflora*, and the subtidal was not vegetated. Water depth was gener-

ally <1 m, but subtidal bottom was always 10 to 20 cm deeper than adjacent intertidal vegetation. Vegetation occurred in irregular patches, creating a reticulated effect on marsh macrostructure, and occupied about 25% of the area (Fig. 2).

Experimental Design

A paired sampling design was employed to compare shrimp densities between marsh habitats. Each sample pair consisted of one sample taken in vegetated habitat and another in adjacent nonvegetated habitat as close as practically possible.

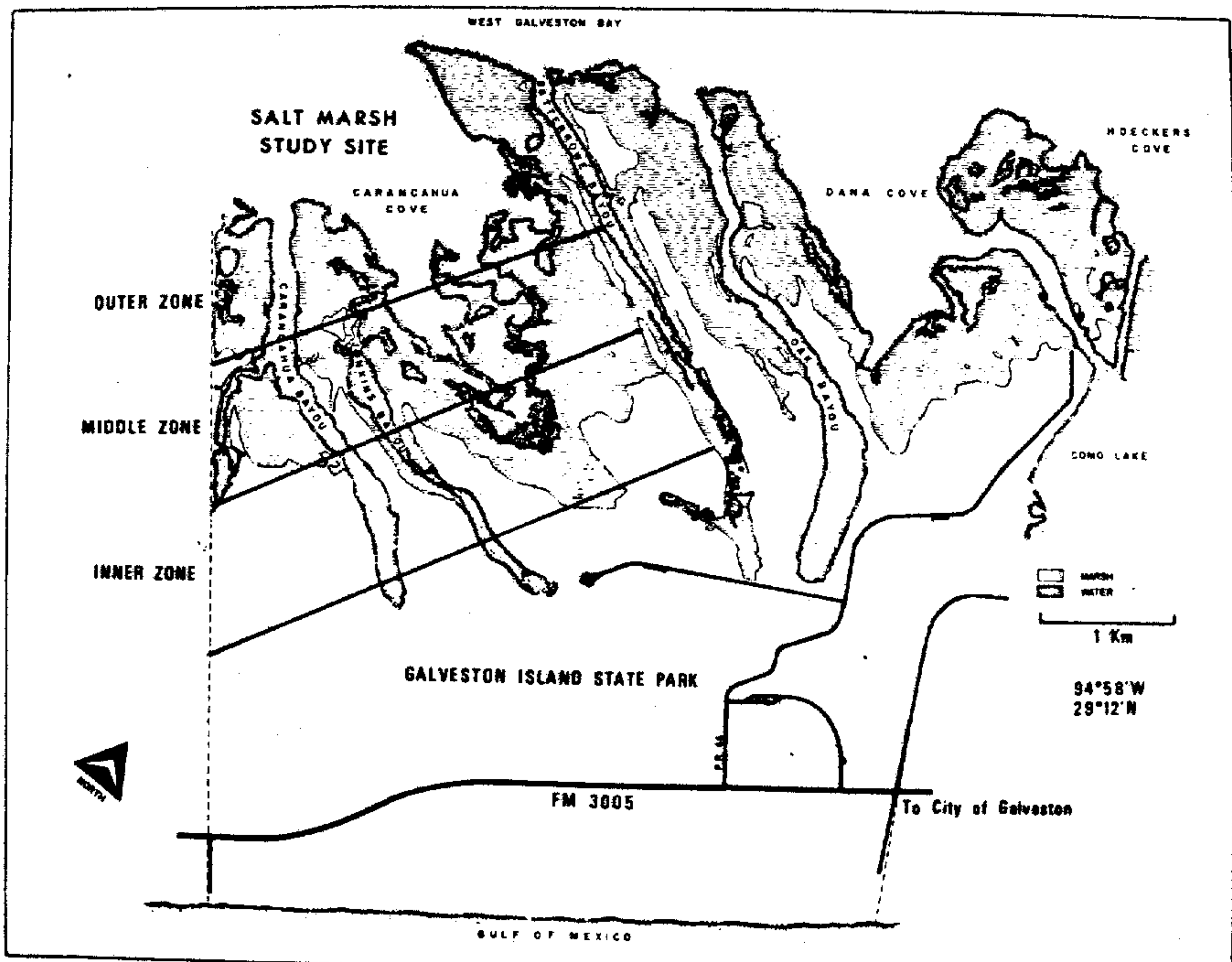Sampling was scheduled to coincide with the

FIGURE 1.—Galveston Island State Park showing the salt marsh study site in Carancahua Cove fronting Galveston West Bay. (Redrawn from Texas Parks and Wildlife Leaflet 4000-42.)

FIGURE 2.—Upper: Reticulation between vegetated and nonvegetated habitats in a salt marsh on Galveston Island. Areal view at about 500 ft altitude. Lower: Stands of intertidal *Spartina alterniflora* and adjacent subtidal nonvegetated bottom in a salt marsh at Galveston Island State Park.

period of maximum seasonal immigration for *P. aztecus* as described by Baxter and Renfro (1967). Accordingly, seven sets of samples were taken between 29 March and 23 July 1982. Each set was obtained over a period of 3 d, and sets were taken biweekly (29 March through 28 May) and monthly (28 May through 23 July). Ordinarily, a set contained 12 sample pairs that were subdivided to sample the inner, middle, and outer marsh zones equally, i.e., during each of three sampling days four vegetated-nonvegetated sample pairs were taken from a single zone. Sample sites within zones were chosen randomly each month from subunits in a grid superimposed on a map of the area. The map and aerial photographs were used to estimate percent coverage of vegetated and nonvegetated habitats within different zones.

A *t*-test of paired observations (Steel and Torrie 1960) provided the primary means for evaluating differences in shrimp density between habitats. Other analyses were performed using Pearson product-moment correlations and ANOVAs across sample sets, and Kendall's nonparametric concordance tests (Tate and Clelland 1957) within sample sets. Analyses across sets incorporated an element of temporal variability that was specifically eliminated in analyses within sets. Data were log transformed for ANOVAs to assure homogeneity of variances.

Procedures

A drop sampler (Fig. 3) was designed to operate in the marsh from the bow of a skiff. The device was an open-ended fiber glass cylinder, reinforced on one end with galvanized metal, that enclosed 2.8 m² of marsh bottom. The sampler was deployed endwise and pushed at least 15 cm into the substrate to insure a good seal against leakage. After marsh grass was removed, water was pumped from the sampler and the enclosed bottom was swept with dip nets to capture the entrapped organisms. The water and the contents of the dip nets were placed into a 1 mm square mesh plankton net with a removable cod end bag. When all sample contents were washed, the cod end bag was detached, labelled, and stored in a container with Formalin[4] and Rose Bengal stain.

Two identical sampling cylinders were used to obtain sample pairs. Typically, the first sampler was hoisted above the bow of the skiff and quietly maneuvered into position over either vegetated or barren substrate. The device was released and allowed to free fall to the bottom. After disconnecting the first sampler, the second sampler was hoisted and the operation repeated in the opposing habitat. The sequence of habitats was reversed from pair to pair so that one would not continually precede the other. Sample pairs were always within two sample diameters of each other (3.6 m) and care was taken to not disturb the site until the second sampler was deployed.

Within all samples, the water temperature,

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[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.
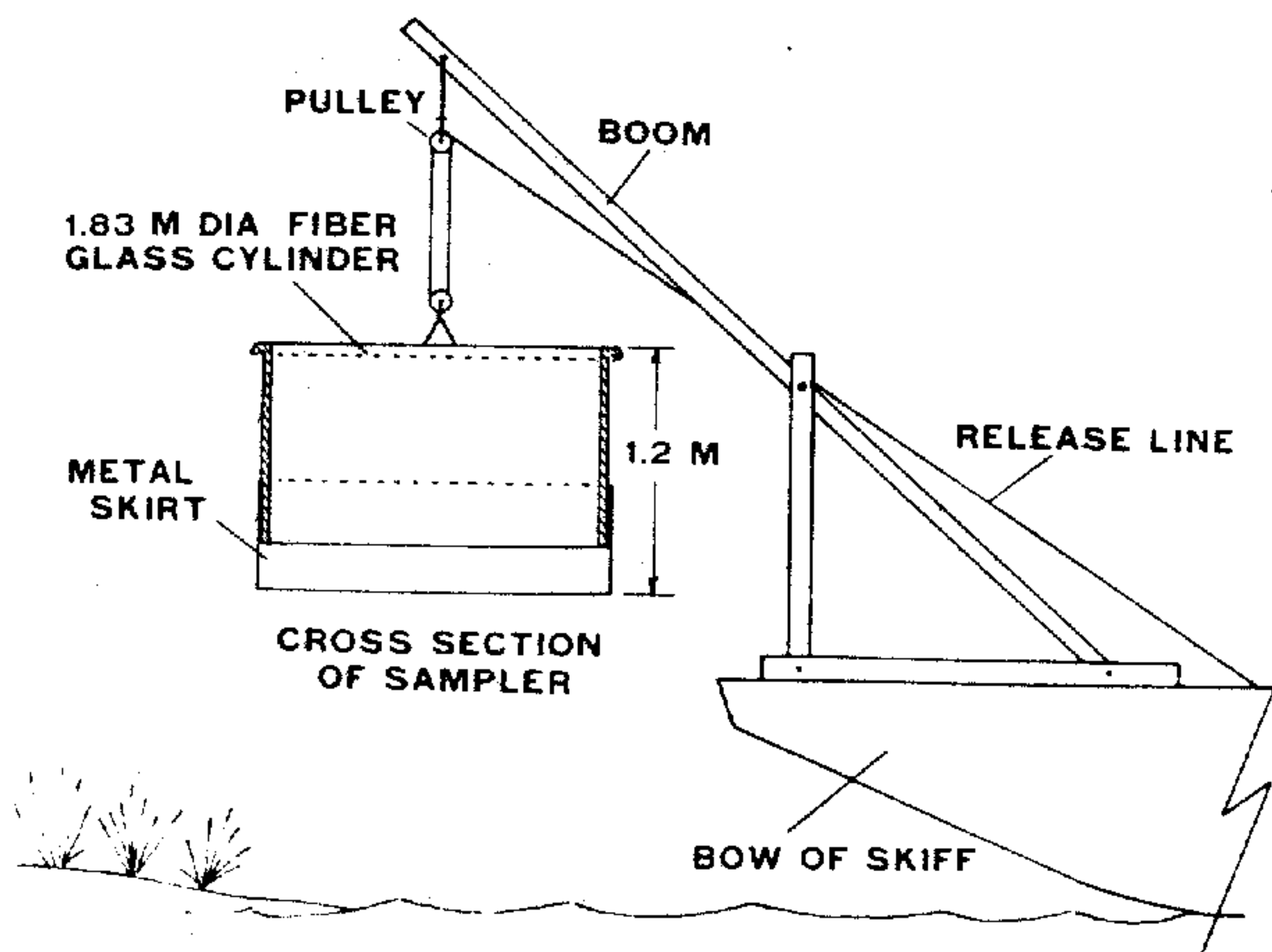

FIGURE 3.—A hand-operated drop sampler used to estimate *Penaeus aztecus* densities in a Galveston West Bay salt marsh.

oxygen (YSI oxygen meter, Model 51 B) and maximum and minimum depth were recorded. Water samples (500 ml) were also procured in order to measure turbidity (HF Instruments, Model DRT-15). In vegetated samples, emergent plant material was cut and removed to measure plant biomass and to facilitate capturing the macrofauna. Tide level was recorded from a permanent station at the beginning and end of each sampling operation. All field work was done during daylight within about 2 h before and after high tide.

In the laboratory, shrimp were identified, sorted, and measured to the nearest millimeter from rostrum tip to end of telson. Shrimp numbers for each millimeter size interval were recorded for each sample. Associated macrofauna from each sample, including fish, crabs, and other shrimp, were identified, measured, and counted. Gut contents of the fish were examined for penaeid shrimp as well as other identifiable material. Plant biomass from each sample was dried in sunlight until weight change was negligible. Sediments and epiphytes were allowed to fall away as the material dried. The resulting dry weight was taken using a Mettler K-7 toploading balance and reported as grams above-ground dry plant biomass. Stem density was calculated by weighing a subsample (about 20% of the total) and counting the number of culms.

Sampler Effectiveness

Since the experimental design assumed no sampling bias, the method was tested for recovery efficiency both in vegetated and nonvegetated habitats. Fifty shrimp, in the size range of 23 to 91 mm, were marked by clipping a uropod and placed into deployed samplers. After a 30-min adjustment period, the usual sampling procedure was followed and recovery was recorded.

Since our density data were compared with other surveys, it was useful to test the effectiveness of the drop sampler in relation to other collecting devices. These included a 1 m beam trawl, a 5.5 m bag seine, and a 3.7 m otter trawl. During the initial test, eight replicate vegetated-nonvegetated sample pairs were taken using the 1 m beam trawl (3.0 m²) and the drop sampler (2.8 m²). Later, 10 nonvegetated sample replicates were obtained for each of the following: the drop sampler, a 5.5 m bag seine (110 m²), and a 3.7 m otter trawl (75 m²). The data were reported as mean and standard deviation of shrimp density

(per m²) for each sampler. The efficiency for each device was calculated relative to the drop sampler.

RESULTS

A total of 3,277 penaeid shrimp (97% *P. aztecus*) were collected in 81 paired samples taken between 29 March and 23 July 1982. Shrimp densities in the marsh were significantly higher in *S. alterniflora* habitat than adjacent nonvegetated habitat ($P < 0.001$, t-test, 81 paired observations). The magnitude and integrity of the relationship between shrimp density and habitat type held consistently throughout all sampling dates (Table 1, Fig. 4) and zones within the marsh, except for the outer zone during March and April (Table 2). Comparison of marsh zones (Table 2) revealed highest *P. aztecus* densities and greater selection for vegetated habitat in the innermost marsh diminishing toward the outer zone. Shrimp densities in nonvegetated habitat were highest in the outer zone and diminished significantly toward the inner zone (ANOVA, $P < 0.001$).

TABLE 1.—Percent of *Penaeus aztecus* in vegetated (*Spartina alterniflora*) and non-vegetated habitats of a Galveston West Bay salt marsh, 29 March through 23 July 1982.

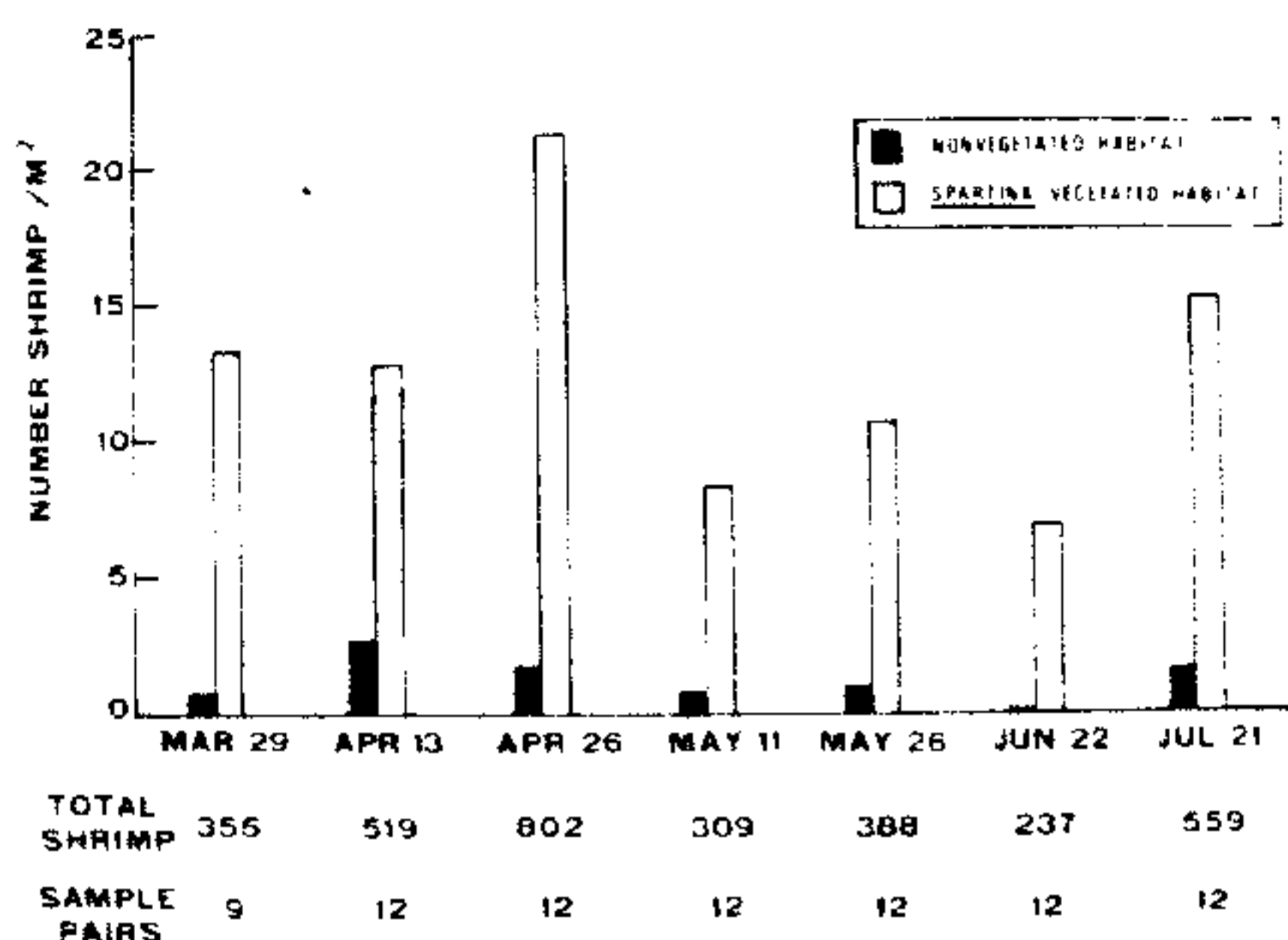| Sampling period	Shrimp number (n)	Habitat	
		Vegetated (% n)	Nonvegetated (% n)
3/29-4/1	355	94.4	5.6
4/13-15	519	81.7	18.3
4/26-28	802	88.3	11.7
5/11-14	309	90.3	9.7
5/26-28	388	91.8	8.2
6/22-24	237	97.0	3.0
7/21-23	559	90.2	9.8

FIGURE 4.—Mean densities of *Penaeus aztecus* compared between vegetated *Spartina alterniflora* habitat and adjacent non-vegetated habitat.

TABLE 2.—Mean number of *Penaeus aztecus* per m² by zone in vegetated and nonvegetated salt marsh habitats from Galveston West Bay 29 March through 23 July 1982.

Sampling period	Marsh zone and habitat			
	Outer Veg/Non[1]	Middle Veg/Non	Inner Veg/Non	Overall Veg/Non
3/29-4/1	[2] 2.7/1.9			
	8.8/5.5	12.3/2.0	16.7/1.1	12.6/2.8
4/26-28	12.3/6.8	28.5/1.3	22.4/0.4	21.1/2.8
5/11-14	7.2/1.2	9.6/1.3	8.0/0.3	8.3/0.9
5/26-28	12.0/1.5	10.6/0.9	9.2/0.4	10.6/1.0
6/22-24	3.8/0.2	9.7/0.3	7.0/0.2	6.8/0.2
7/21-23	10.9/1.8	13.8/1.9	20.3/1.3	15.0/1.6
Overall	7.5/2.3	11.0/1.0	16.6/0.6	11.7/1.4

[1] Veg = *Spartina alterniflora* habitat; Non = Nonvegetated habitat.
[2] Difference within brackets not significant between vegetated and nonvegetated pairs; for all others, the difference was highly significant ($P < 0.001$, t-test, paired observations).

Penaeus aztecus densities for each 20 mm size interval were more abundant in *Spartina* habitat than adjacent nonvegetated bottom (Fig. 5). Vegetated habitat contained 89 to 96% of all shrimp in size classes under 50 mm and 75 to 78% of larger size classes (Table 3). Those under 30 mm in length comprised 77,% of all shrimp and those under 60 mm made up 98% of the total (Table 3). Size class distributions differed between habitats (Kolmogorov-Smirnov test, $P = 0.02$; Fig. 5), but the very small sample size from nonvegetated habitat decreased the strength of this observation.

The highest *P. aztecus* densities in vegetation and the lowest on nonvegetated bottom were characteristic of the innermost zone (Table 1). The degree of vegetated-nonvegetated differences suggested an apparent selection for vegetated

habitat and greater selection in the inner zone compared with the outer zone. The increase in vegetated to nonvegetated shrimp densities coincided with an increase in *S. alterniflora* coverage between the outer and inner marsh (Fig. 6). Areal coverage of vegetation, determined from aerial photographs (Fig. 2), differed by a factor of 3 between the outer and inner marsh, and selection, as measured by the ratio of shrimp density in vegetated habitat to density in nonvegetated habitat, differed by a factor of 9 from outer to inner zones (Fig. 6). In addition, the ratio differed between the middle and inner zone, but shrimp densities within vegetation between those zones (Table 2) did not change significantly (ANOVA, Duncan's multiple range test, 0.05 level). Due to the intertidal nature of vegetated habitat, shrimp were forced into subtidal areas at low tide and redis-

TABLE 3.—Percent abundance among size classes for *Penaeus aztecus* in a Galveston West Bay salt marsh, 29 March through 23 July 1982. n = number of shrimp per size interval; N = total number of shrimp collected.

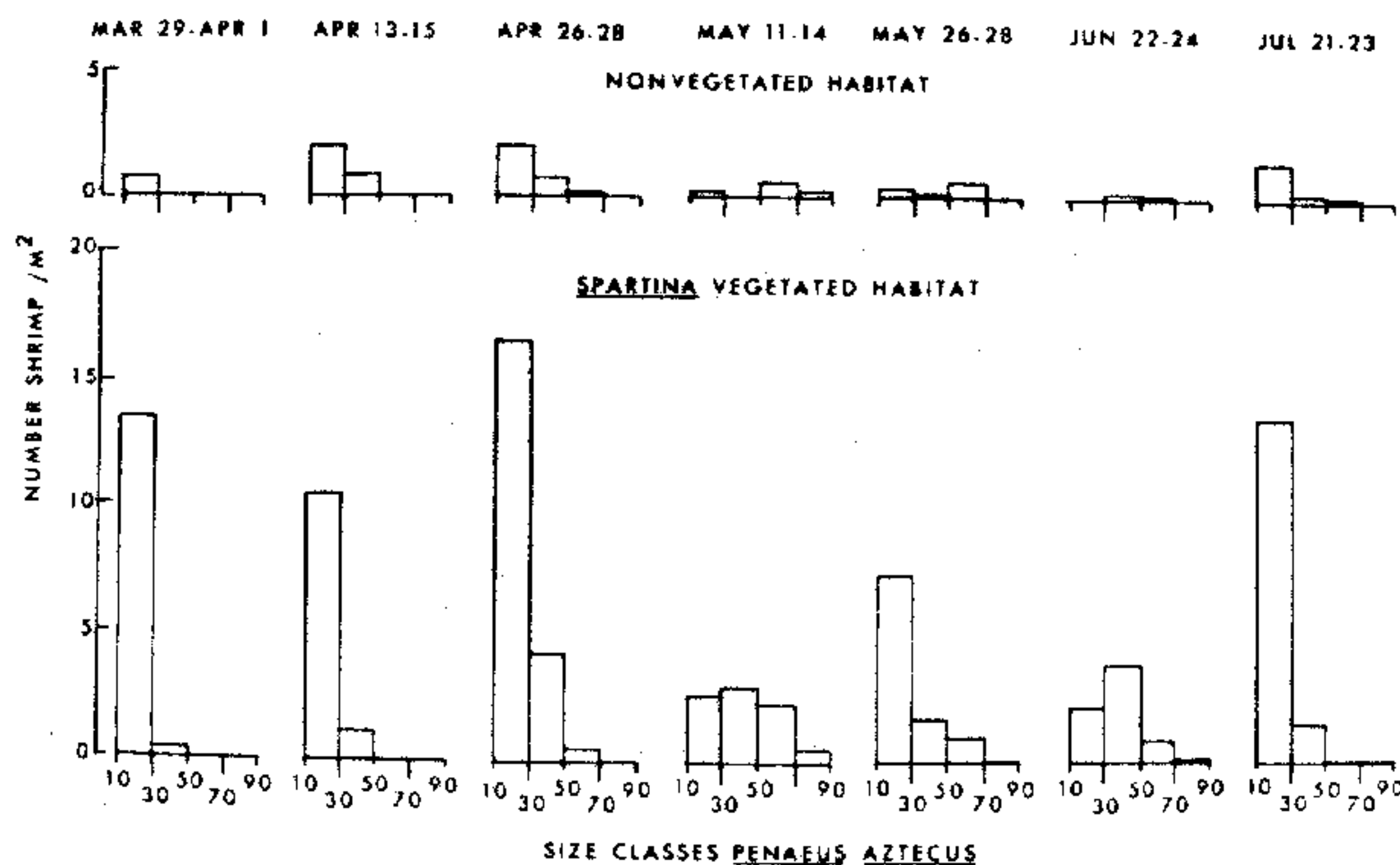| Size class (mm)	Shrimp abundance				
	Overall			Spartina	Nonvegetated
	n	% N	Cum. %	(% n)	(% n)
<20	1,117	47.7	47.7	89.4	10.6
21-30	683	29.2	76.9	95.6	4.4
31-40	234	10.0	86.9	94.9	5.1
41-50	184	7.8	94.7	88.6	11.4
51-60	86	3.7	98.4	77.9	22.1
61-70	25	1.1	99.5	76.0	24.0
71-80	8	0.3	99.8	75.0	25.0
81-90	4	0.2	100	75.0	25.0
Total (N) = 2,341					

FIGURE 5.—Densities of *Penaeus aztecus* by size class in adjacent vegetated and nonvegetated habitats from Galveston West Bay during 1982. Size class distributions differed between habitats (Kolmogorov-Smirnov test, $P = 0.02$).
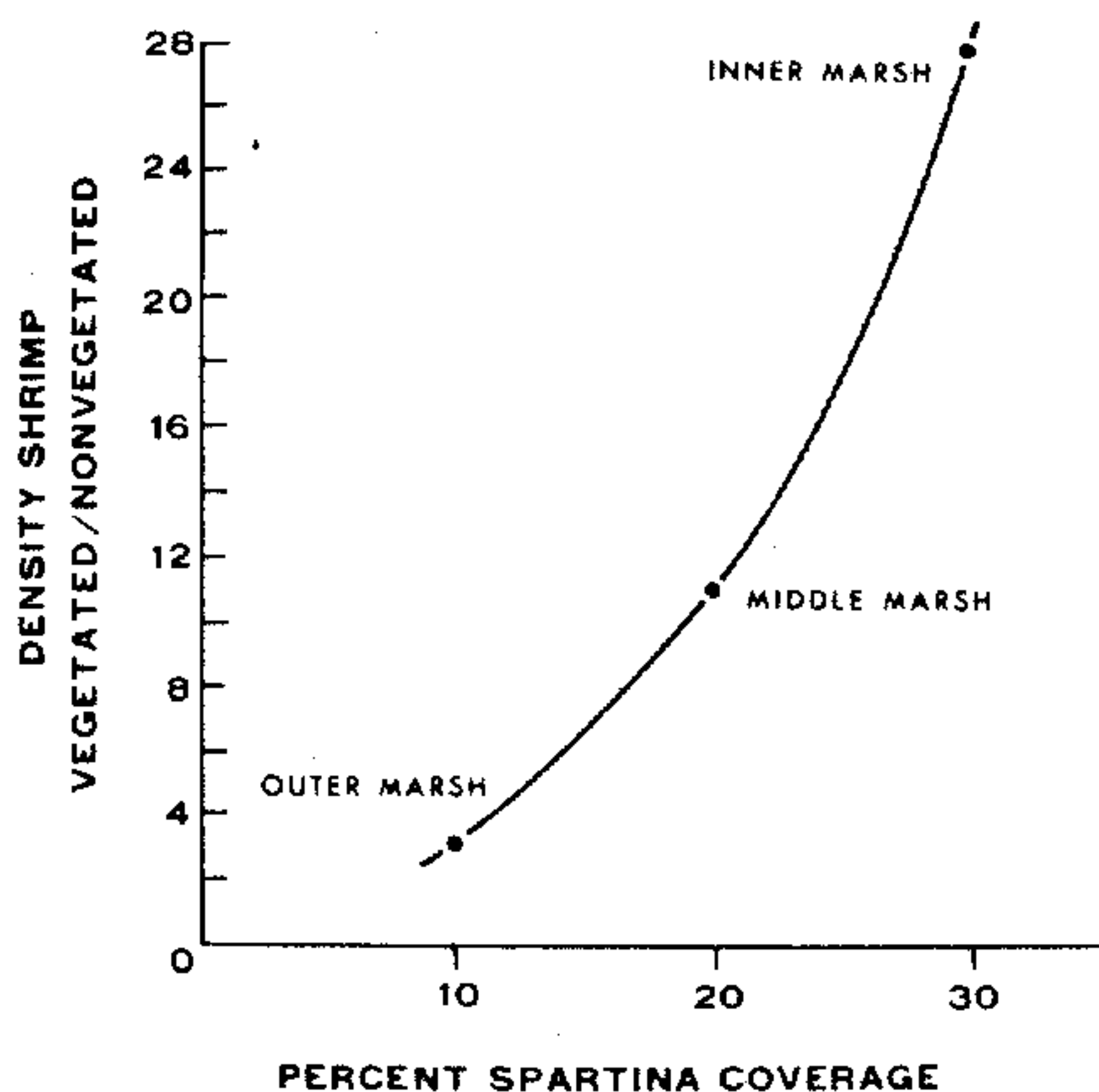
FIGURE 6.—Selection by *Penaeus aztecus* for vegetated habitat compared against percent coverage of *Spartina alterniflora*.

TABLE 4.—Within habitat densities of *Penaeus aztecus* from a salt marsh in Galveston West Bay, 29 March through 23 July 1982. *n* = number of samples.

Marsh habitat and zone	n	Individuals/m²				
		$\bar{x}$	Median	1 SD	Coeff. var. (%)	Range
With vegetation						
Outer	27	7.5	6.4	6.8	90	0.7-28.2
Middle	26	11.0	11.4	8.9	81	0.4-39.6
Inner	28	16.6	13.8	12.5	75	1.8-43.2
Overall	81	11.7	10.5	9.4	80	0.7-43.2
Without vegetation						
Outer	27	2.3	1.4	3.6	157	0-18.2
Middle	26	1.0	0.7	1.2	120	0- 4.6
Inner	28	0.6	1.0	1.5	56	0- 2.1
Overall	81	1.4	1.1	1.9	136	0-18.2

tributed anew on each subsequent flood tide.

Differential predation by fish did not account for shrimp differences between habitats. Of four species preying on shrimp, 328 were in vegetation versus 48 on nonvegetated bottom. Among these, 18 from vegetated (5%) and 3 from nonvegetated (6%) contained shrimp in gut contents. The predators, in order of vegetated/nonvegetated abundance, were *Lagodon rhomboides* (pinfish 246/36), *Fundulus grandis* (gulf killifish 45/0), *Cynoscion nebulosus* (spotted seatrout 22/2), and *Paralichthys lethostigma* (southern flounder 15/10). Only southern flounder contained shrimp in gut contents (3 of 10) from nonvegetated habitat. In vegetated habitat, 8 of 15 southern flounder, 10 of 22 spotted seatrout, 1 of 45 gulf killifish, and 3 of 246 pinfish contained shrimp.

Mean density of *P. aztecus* in vegetation was 11.7/m² overall with a range of 0.7 to 43.2/m² (Table 4). Densities were highest in the innermost marsh ($\bar{x}$ = 16.6/m²; range = 1.8 to 43.2/m²) and lowest in the outer marsh ($\bar{x}$ = 7.5/m²; range = 0.7 to 28.2/m²). The overall variance was less than the overall mean. Among marsh zones, shrimp patchiness in vegetation decreased slightly from the outer to inner marsh (Table 4).

Density of *P. aztecus* in nonvegetated habitat was 1.4/m² with a range of 0 to 18.2/m² (Table 4). Densities on nonvegetated bottom were highest in the outer marsh ($\bar{x}$ = 2.3/m²; range = 0 to 18.2/m²) and lowest in the inner marsh ($\bar{x}$ = 0.6/m²; range =

0 to 2.1/m²). Overall distribution on nonvegetated bottom, as reflected by the variance to mean ratio (coefficient of variation, Table 4), was patchier (more clumped) than on vegetated bottom. Shrimp distributions also were patchier in nonvegetated outer and middle zones, than in the nonvegetated inner zone.

Stem density and above-ground biomass of *S. alterniflora* were positively correlated (Table 5). The overall range of values was 41 to 784 g/m² for biomass and 33 to 629 stems/m² with respective means of 298 g/m² (1 SD = 175, *n* = 81) and 234 stems/m² (1 SD = 72, *n* = 81). Between zones, plant biomass from the outer to inner zone increased from 258 to 348 g/m². The weight per stem increased (larger diameters) from outer to inner marsh. Although the trend suggested a negative relationship between shrimp density and vegetational density and biomass, correlation was not significant over the range examined.

Abiotic Relationships

Water depth between vegetated and nonvegetated sample pairs was significantly different (*P* < 0.01, *t*-test of 81 paired observations). The mean water depth was 22.1 cm (1 SD = 10.0, *n* = 81) in

TABLE 5.—Density and biomass of *Spartina alterniflora* from a salt marsh in Galveston West Bay, 29 March through 23 July 1982. *n* = number of samples.

Biomass and density	n	$\bar{x}$	1 SD	Coeff. var. (%)	Range
Biomass (g/m²)					
Outer zone	27	258	164	64	41-634
Middle zone	26	289	187	65	41-784
Inner zone	28	348	174	50	69-731
Overall	81	298	175	59	41-784
Density (stems/m²)					
Outer zone	28	234	88	38	37-576
Middle zone	26	231	65	28	33-629
Inner zone	28	236	64	27	47-496
Overall	81	234	72	31	33-629

vegetated samples compared with 41.8 cm (1 SD = 11.8, n = 81) in nonvegetated samples. Changes in tide level were not large (about 30 cm) but were important relative to sample depths. Since sampling was executed at high tide, tide station measurements were comparable between sampling periods and useful for establishing variability in high-water level. Mean high water during the summer was 12 cm lower than in the spring reflecting seasonally variable tidal inundation (Hicks et al. 1983) and greater accessibility to vegetation (Provost 1976) in the spring.

A weak negative relationship between shrimp density and temperature within a range of 17.0° to 34.0°C was apparent (r = −0.34 in vegetation, $P <$ 0.01, n = 57). Since temperature and oxygen levels were inversely related, the trend, attributed to temperature, also extended to an observed relationship between oxygen concentration and shrimp density. However, oxygen levels were always near saturation (vegetated $\bar{x}$ = 8.2 ppm, 1 SD = 1.4, n = 81; nonvegetated $\bar{x}$ = 8.1 ppm, 1 SD = 1.4, n = 81) and unlikely to have influenced shrimp distribution. Shrimp densities did not correlate well with salinities (range of 19 to 35 ppt), turbidities (range of 3.0 to 55 nephelometer turbidity units), or water depths (overall range of 5.5 to 76 cm). In addition, temperature, salinity, oxygen, and turbidity did not differ between habitats (t-test of 81 paired observations for each).

Sampler Performance

Test results suggested that shrimp recovery from the drop sampler was more variable and somewhat less effective in vegetation ($\bar{x}$ = 91% recovery, 1 SD = 6.6%, n = 4) than in habitat without vegetation ($\bar{x}$ = 97.5% recovery, 1 SD = 2.5%, n = 4). However, a t-test between means by habitat revealed no significant difference ($P >$ 0.1) and justified combining means (94%, 1 SD = 5.8%, n = 8).

Mean shrimp densities on nonvegetated bottom, comparing our 1.8 m diameter drop sampler, a 5.5 m wide bag seine, and a 3.7 m wide otter trawl, were 0.285/m², 0.104/m², and 0.054/m², respectively. Assuming 97.5% recovery and no avoidance with the drop sampler, conservative estimates of efficiency were 33% for the bag seine and 17% for the otter trawl. Clearly, the data from the drop sampler were more accurate (Table 6).

DISCUSSION

Habitat Selection

Significant differences in habitat-related shrimp densities from a Galveston salt marsh (Table 2, Fig. 4) demonstrate that *P. aztecus* may select for *S. alterniflora* habitat. In support, laboratory data of Giles and Zamora (1973) suggest that *P. aztecus* and *P. setiferus* each prefer *S. alterniflora* as opposed to barren substrate. In addition, marsh grass transplanted on a dredge spoil in Galveston Bay increased shrimp numbers (Trent et al. 1969) and elimination of marsh habitat to create waterfront housing diminished shrimp abundance (Mock 1966; Gilmore and Trent 1974; Trent et al. 1976). In other instances, *P. aztecus* has been associated with vegetation including *Ruppia* and *Vallisneria* in Mobile Bay (Loesch 1965), seagrasses in the Laguna Madre (Stokes 1974), and *Juncus, Spartina,* and seagrasses in Mississippi Sound (Christmas et al. 1976). The latter reported movement of postlarvae into marsh vegetation during tidal inundation.

The determinants of selection may have less to do with *S. alterniflora* per se than with other characteristics of vegetated habitat. For example, in our case, shrimp numbers were not related to the density or biomass of marsh grass (Table 5) but simply to its presence or absence. Also, attraction to vegetation differed between outer and inner marsh (Table 2). Other studies have shown that

TABLE 6.—Comparative gear efficiencies for sampling *Penaeus aztecus* in a Galveston West Bay salt marsh. Area sampled and number of replicates for each device are as follows: Drop sampler 2.8 m² (n = 22); beam trawl 3.0 m² (n = 12); bag seine 109 m² (n = 10); otter trawl 72 m² (n = 10).

Habitat type	$\bar{x}$ Efficiency			
	Drop sampler	Beam trawl	Bag seine	Otter trawl
Spartina vegetation	94%	23%	not operable	not operable
(Shrimp count, $\bar{x}$/m² ±SD)	(8.9 ±3.7)	(2.2 ±2.2)		
Nonvegetated	98%	82%	33%	17%
(Shrimp count, $\bar{x}$/m² ±SD)	(0.30 ±0.3)	(0.25 ±0.46)	(0.10 ±0.06)	(0.05 ±0.04)

the presence of estuarine macrophytes can be associated with an increase in epifaunal abundance (Heck and Wetstone 1977; Heck and Orth 1980) as well as providing protective cover (Vince et al. 1976; Nelson 1979; Coen et al. 1981; Heck and Thoman 1981). For shrimp selecting vegetated marsh, this may translate into a greater variety and abundance of food and some degree of protection from predation.

Zonal and Areal Relationships

Penaeus aztecus demonstrated a greater degree of attraction to vegetated habitat in the inner than the outer marsh. Accordingly, shrimp densities were higher among vegetation and lower on nonvegetated bottom in the innermost zone compared with the outer zone. This relationship is adequately reflected by comparing ratios of vegetated with nonvegetated shrimp density. Using the ratios, the change in selection from the outer, middle, to inner zone was 3.3:1, 11.0:1, and 27.7:1, respectively. The percent area covered by *S. alterniflora* (Fig. 2) also increased (by a factor of three) from outer to inner marsh, but as vegetational coverage increased arithmetically selection by *P. aztecus* increased geometrically (Fig. 6). This implies that salt marshes with more vegetational coverage have disproportionately greater attractive value to *P. aztecus* than do those with less coverage. On a larger scale, Turner (1977) revealed a positive correlation between extensiveness of estuarine vegetation and offshore shrimp yield. However, the relationship may not be simple; it is likely to depend upon characteristics such as the configuration, accessibility, and quality of vegetational patches within a marsh. For instance, an edge effect has been identified which associates large numbers of shrimp with the nonvegetated zone adjacent to vegetation (Mock 1966; Christmas et al. 1976). Since our *Spartina* habitat was intertidal, and often not inundated during low tides, the nonvegetated subtidal habitat provided a refuge against stranding. We have assumed that it did and that shrimp redistributed accordingly each tidal cycle. It is evident that an increase in the amount of ecotone edge (between habitats) would facilitate movement for the shrimp population. It is also evident that the amount of edge is proportionally related to the degree of reticulation in the marsh (Fig. 2). Thus, reticulation may be an important mechanism for increasing the accessibility of intertidal vegetation to *P. aztecus*.

Shrimp Densities

Density estimates for penaeid shrimp in *S. alterniflora* vegetation have not been reported previously. We found a density range for *P. aztecus* in *Spartina* habitat of 0.7 to $43.2/m^2$ with an overall mean, from March through July, of $11.7/m^2$ (1 SD = 9.4, $n = 81$). Comparable densities from adjacent nonvegetated habitat ranged between 0 and $18.2/m^2$. All densities were taken when *P. aztecus* numerically dominated the shrimp population. By August, when *P. setiferus* first began to dominate, the combined mean for both species in vegetation increased to $50.8/m^2$ (1 SD = 31.6, $n = 12$) and a single sample attained a density of 118.6 shrimp/m^2. These data may indicate a potential for higher *P. aztecus* densities earlier in the season and suggest that *P. aztecus* were not restricted by lack of space.

To our knowledge, we have provided the first accurate estimates of shrimp density in marsh vegetation, and our densities are among the few available for any estuarine system. Due to method limitations, most researchers have only reported relative abundances of restricted sizes, usually over nonvegetated bottom. The single exception was data by Allen and Hudson (1970), using a suction sampler in seagrasses in Florida Bay. From 43 trials, they reported a mean of $6.2/m^2 \pm$ 3.4 SD for *P. duorarum*.

Estimates of *P. aztecus* densities from nonvegetated bottom in three other Galveston Bay salt marshes were available from the Texas Parks and Wildlife Department (TPWD) from 1976 through 1981 (Benefield 1982, footnote 5.). The data were taken using a marsh net (Renfro 1963) which was relatively effective for capturing shrimp on nonvegetated bottom (Table 6 compares a beam trawl, similar to the marsh net, with other sampling devices). Mean TPWD densities for *P. aztecus* during the latter half of March were $10.4/m^2$ for 1976, $5.2/m^2$ for 1977, $0.3/m^2$ for 1978, $1.3/m^2$ for 1979, $8.7/m^2$ for 1980, and $5.1/m^2$ for 1981 with an overall mean of $5.2/m^2$. In our study, on nonvegetated bottom, the March mean for *P. aztecus* was $0.9/m^2$ and overall (March through July) the mean was $1.4/m^2$. It is evident that our nonvegetated densities for *P. aztecus* were within the range, but low compared with the mean calculated from TPWD data.

These densities of *P. aztecus* may not be strictly

comparable, since sampling was executed during unknown variable tidal stages and the degree of flooding in intertidal vegetation appears to greatly influence shrimp densities on nearby non-vegetated subtidal bottom. Perhaps the only meaningful density estimates are those taken during low tide in nonvegetated habitat or those taken in vegetated habitat at flood tide. In any case, tide stage must be uniform for data to be comparable.

Sampling Integrity

The sampling approach in our investigation provided more realistic density estimates than traditional methods for sampling shrimp in estuaries (Table 6). We agree with Loesch et al. (1976) in concluding that techniques such as the area-swept method using an otter trawl are among the poorest for quantifying *P. aztecus*. Past recognition of this problem stimulated development of the push net (Allen and Inglis 1958), small beam trawl (Renfro 1963; Loesch 1965), and marsh net (Pullen et al. 1968). These samplers improved accuracy on nonvegetated bottom, but were ineffective when vegetation was present and did not solve avoidance problems. Further improvement came for sampling in seagrasses, but not salt marshes, with the invention of a sled-mounted suction sampler (Allen and Hudson 1970) and modification of a drop net technique (Hoese and Jones 1963; Gilmore et al. 1976). Our methodology has been designed to minimize escape, improve recovery from the area sampled (including burrowed shrimp), and to operate in salt marsh habitats. The drop-sampler method proved to be nearly as effective among vegetation as on nonvegetated bottom.

CONCLUSION

We contend that differences in *P. aztecus* densities between vegetated and nonvegetated marsh bottom were due to habitat selection. In support, we refer to Loesch (1965), Trent et al. (1969), and Stokes (1974) who have associated brown shrimp distributions with estuarine vegetation, and a laboratory experiment by Giles and Zamora (1973) demonstrating *P. aztecus* prefer *S. alterniflora* instead of barren substrate. Finally, our fish gut examinations indicate that immediate effects of predation did not account for the density differential.

Since *S. alterniflora* is characteristically intertidal, and not continuously available to shrimp,

the adjacent subtidal zone provided an important alternate habitat during low tide. We propose that the amount of edge between habitats facilitated shrimp movement, and the reticulated nature of the salt marsh was an important feature for increasing the amount of edge. In addition, intertidal vegetation was more accessible and its potential for utilization greater during spring and fall high tides. This interaction may in part account for seasonal peaks in *P. aztecus* populations. In our investigation, recruitment began abruptly with equinox tides. The shrimp population during the spring and early summer was dominated entirely by *P. aztecus*.

Our shrimp densities from vegetated habitat were higher than any previously reported including those from seagrass and mangrove systems. The high densities in vegetation were possibly governed by the amount of total marsh, ratio of vegetated to nonvegetated habitat, and size of recruitment. The densities on nonvegetated marsh bottom were probably controlled by the relative accessibility of nearby vegetated habitat. In any case, the observed density differential strongly implies that marsh vegetation provides a vital function for juvenile brown shrimp.

ACKNOWLEDGMENTS

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